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Temporal Variability of the Nutrient Environment on Davies Reef in the Central Great Barrier Reef, Australia[1]

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ABSTRACT: Nutrient concentrations were measured at a fixed station in the lagoon of Davies Reef, the central Great Barrier Reef, Australia, monthly between January and December 1990. The day-to-day variation in nutrient concentration inside and outside the lagoon was determined in May. The average dissolved inorganic nitrogen (DIN) (sum of NO_3, NO_2, and NH_4) concentration for the pooled data in each of 11 monthly observations ranged between 0.34 and 1.84 μM. There was only a two-fold variation in average PO_4 concentration. Average SiO_4 concentration showed a magnitude of variation similar to that of DIN concentration. DIN concentration was significantly higher in the lagoon than in the surrounding open water, suggesting that the significant DIN flux results from internal sources. There were no clear inside-outside differences in PO_4 and SiO_4 concentrations. N:P ratios in the lagoon were usually $<16:1$, suggesting the possibility of N limitation. However, the ratios became $>16:1$ under low wind conditions, when the exchange of lagoon water was restricted and the contribution of the internal DIN flux to the nutrient budget increased. Si was usually available in excess of the growth requirement of diatoms (Si:N $> 1:1$), but occasional decreases in relative Si availability resulted in occurrence of a high number of dinoflagellates.

INCREASED AGRICULTURAL activities and coastal development in northeastern Australia have raised concern about the effect of elevated nutrient concentrations on coral reefs in the Great Barrier Reef (GBR). However, the range of nutrients that coral reefs in the GBR actually experience has not been resolved fully (e.g., Hatcher and Hatcher 1981, Crossland and Barnes 1983, Hatcher and Frith 1985), thus causing an obstacle to ascertaining the distinction between natural variation and anthropogenic impacts.

Marine phytoplankton take up C, N, and P at ca. 106:16:1 by atoms (Redfield 1958, Goldman et al. 1979). It has been considered, based on the Redfield ratio, that phytoplankton is generally limited by N rather than P (Ryther and Dunstan 1971), although the extent of N limitation is still open to debate (cf. Hecky and Kilham 1988). There has been a similar argument over Si limitation of the growth of diatoms (Officer and Ryther 1980), which require N and Si at ca. 1:1 (Redfield 1958). The relative abundances of inorganic nutrients exert a strong influence on phytoplankton communities and trophodynamic processes, and therefore have been recognized as one of the critical aspects in marine system management (Hecky and Kilham 1988, Turner and Rabalais 1991).

On coral reefs, the fixation of atmospheric N by benthic algal communities makes an important contribution to nutrient budgets (e.g., Johannes and Project Symbios Team 1972, Wiebe et al. 1975, Larkum et al. 1988). High concentrations of inorganic nutrients, particularly NH_4, have been observed in reef sediments (Entsch et al. 1983) and framework (e.g., Andrews and Muller 1983, Sansone 1985, Tribble et al. 1990). Water, as it flows over coral reefs, becomes enriched with dissolved inorganic nitrogen (DIN) (e.g., Hatcher and Hatcher 1981, Wilkinson et al. 1984, Hatcher and Frith 1985), probably re-

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flecting these large internal N sources. On the other hand, no such increase is observed for P (Pilson and Betzer 1973). The possibility of P limitation of algae, both planktonic and benthic, in reef lagoons has been suggested (Atkinson and Smith 1983, Smith 1984, Sorokin 1990).

In this study, I measured the temporal variability of inorganic N, P, and Si in the lagoon of Davies Reef in the central Great Barrier Reef and attempted to characterize its nutrient environment in relation to the stoichiometric requirement of phytoplankton. This type of baseline study is required to develop monitoring strategies and management plans for individual coral reefs.

MATERIALS AND METHODS

Davies Reef is a platform reef (ca. 6 km long, 3 km wide) on the inner edge of the GBR reef matrix off Townsville (Figure 1). A fixed sampling site located in the northeastern corner of the lagoon was surrounded by an extensive area of the reef flat.

Water samples for nutrient and chlorophyll *a* (hereafter called chl. *a*) analyses and dinoflagellate counts were collected monthly between January and December 1990. Sampling was usually carried out at midday, midnight, and the following morning (0800–1200 hr). Samples were collected with an acid-washed 5-l Niskin bottle from 0, 3, 6, and 9 m depth and 1 m above the bottom (11–13 m, depending on tides). Duplicate 10-ml subsamples were filtered through 0.4-μm filters (Acrodisc, Gelman Sci.) and stored frozen for later analysis of inorganic nutrients. Subsamples (100 ml) for chl. *a* analysis were filtered onto Whatman GF/F filters, which were then frozen. One-liter subsamples were preserved with a borax-neutralized formalin solution at a final concentration of 1% for later dinoflagellate counts.

In April, nutrient and chl. *a* samples were collected over a 24-hr period at times corresponding to low, midflood, high, and midebb tides. The day-to-day variations in nutrient concentration in the lagoon and the surrounding open water were observed from 6 to 13 May. Samples were obtained at midday

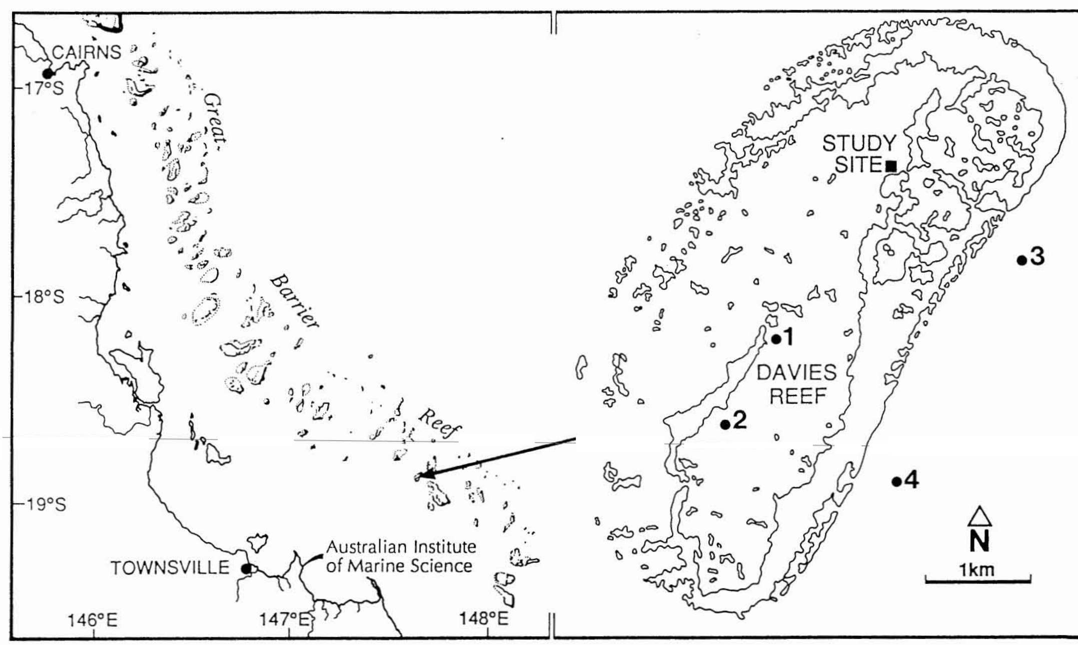

FIGURE 1. Location of sampling sites on Davies Reef (shown enlarged at right) in the central Great Barrier Reef. Study site is the site of the diel and seasonal samplings and stations 1–4 are the sites for the daily sampling.

from 0, 5, 10, and 15 m depth at two lagoon sites (stations 1 and 2) and from 0, 20, and 50 m depth at two open-water sites (stations 3 and 4) (Figure 1).

Nutrient samples were analyzed for NO_3, NO_2, NH_4, PO_4, and SiO_4 using a multichannel segmented flow analyzer (Ryle et al. 1981). Chl. *a* concentration was determined by fluorometry (Strickland and Parsons 1972). Formalin-preserved samples were allowed to stand for 24 hr and concentrated about 10-fold by slowly siphoning off the supernatant. Dinoflagellates in 1/10 of the concentrates were counted under an inverted microscope.

TABLE 1

RELATIVE ABUNDANCE (MEAN ± 1 SD) OF DISSOLVED INORGANIC N, P, AND SI IN DAVIES REEF LAGOON

DATE	NO. OF SAMPLES	N:P	SI:N	SI:P
5 Jan.	10*	22.0	0.4	8.5
29 Jan.	15	5.3	1.0	5.3
5 Mar.	15	4.4	1.6	7.2
5 Apr.	40	23.0	0.8	18.3
26 Apr.	15	5.1	0.9	4.8
24 May	10*	4.1	2.1	9.0
9 July	5†	4.3	2.8	12.1
6 Aug.	15	3.7	3.5	12.7
3 Sept.	15	4.0	3.9	15.6
1 Nov.	5†	5.3	1.6	8.4
4 Dec.	5†	4.9	1.1	5.1

*No midnight samples.
†Midday samples only.

RESULTS

Figure 2 presents the average DIN (sum of NO_3, NO_2, and NH_4), PO_4, and SiO_4 concentrations for each of 11 monthly observations. DIN concentration was between 0.34 and 1.84 μM, with NH_4 accounting for 38–55% of the sum. There was only a two-fold variation in PO_4 concentration (0.07–0.15 μM). SiO_4 concentration (0.36–1.56 μM) showed a magnitude of variation similar to that of DIN concentration. Table 1 summarizes the relative abundance of N, P, and Si by atoms. Usually, N:P ratios were < 16:1 (the Redfield ratio), but the elevated N concentration on 5 January and 5 April resulted in high N:P ratios. The elevated N concentration on these two occasions was also reflected in low Si:N ratios.

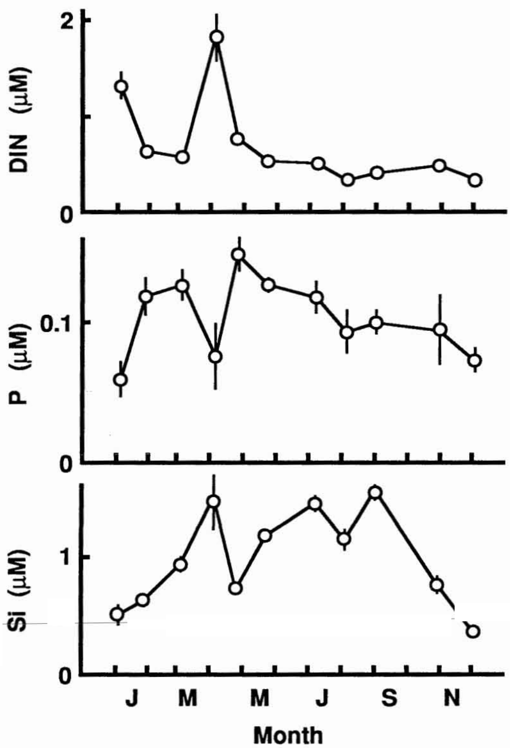

FIGURE 2. Seasonal variations in depth-averaged DIN ($NO_3 + NO_2 + NH_4$), PO_4, and SiO_4 concentrations in Davies Reef lagoon. Vertical lines denote standard deviation of the mean.

The difference in nutrient concentration between midday and midnight was tested using the pooled data during monthly observations (Table 2). There was a significant

TABLE 2

TWO-SAMPLE *t* TEST FOR MIDDAY AND MIDNIGHT CONCENTRATIONS OF DISSOLVED INORGANIC N, P, AND SI IN DAVIES REEF LAGOON

NUTRIENT	df	*t* VALUE	*P**
N	58	2.894	0.007
P	58	2.494	0.019
Si	58	0.839	0.408

NOTE: No. of samples = 30.
*Two-tailed hypothesis, H_0: $u_1 = u_2$.

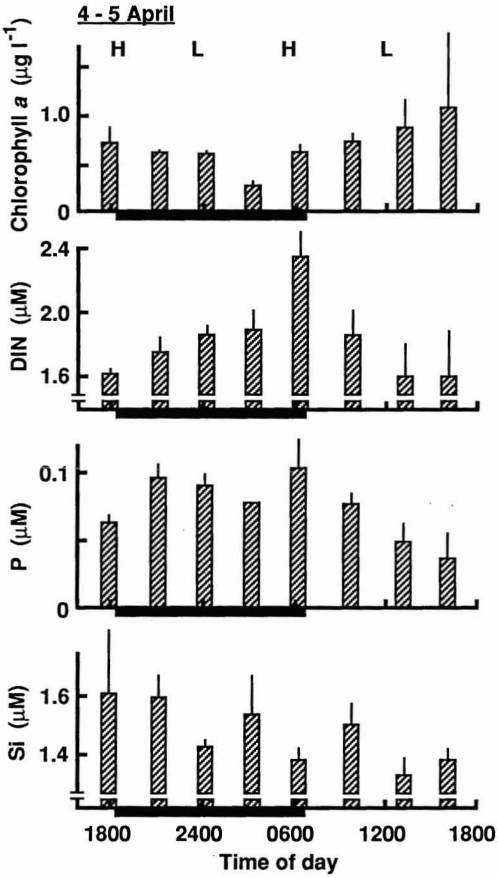

FIGURE 3. Diel variations in depth-averaged chlorophyll *a*, DIN ($NO_3 + NO_2 + NH_4$), PO_4, and SiO_4 concentrations in Davies Reef lagoon. Vertical lines denote standard deviation of the mean. Heavy horizontal line denotes nighttime hours. H, high tide; L, low tide.

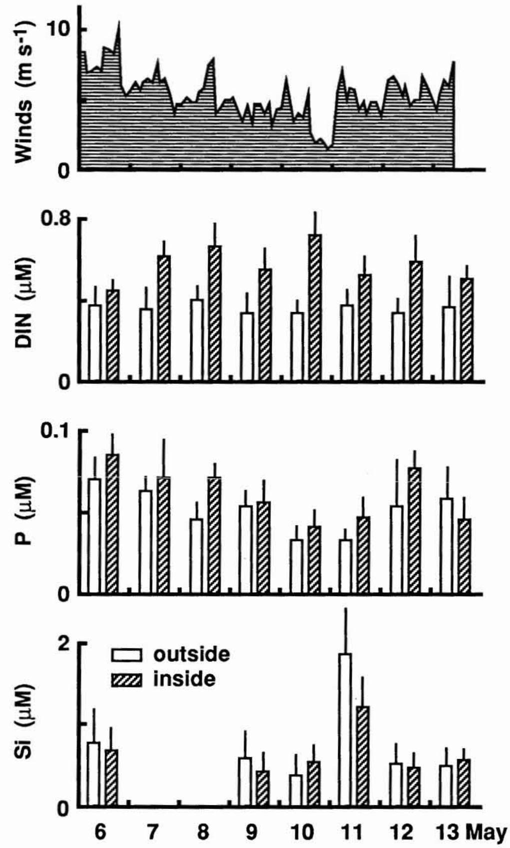

FIGURE 4. Day-to-day variations in wind speed, DIN ($NO_3 + NO_2 + NH_4$), PO_4, and SiO_4 concentrations inside and outside Davies Reef lagoon (stations 1–2 and stations 3–4, respectively). Vertical lines denote standard deviation of the mean.

day-night difference in concentrations of DIN and PO_4 (midday < midnight), but not in SiO_4 concentration.

The diel variations in depth-averaged concentrations of chl. *a*, DIN, PO_4, and SiO_4 are shown in Figure 3. The effect of tides on these parameters could not be detected. Chl. *a* concentration was significantly higher during the day than at night ($t = 3.707$; df = 19; $P < 0.005$). The concentrations of DIN and PO_4, on the other hand, were again significantly higher at night than during the day ($t = 3.187$; df = 19; $P < 0.005$ and $t = 6.090$; df = 19; $P < 0.001$, respectively). There was no significant day-night difference in SiO_4 concentration ($t = 0.453$; df = 19; $P > 0.5$). The concentrations of PO_4 and SiO_4 tended to decrease over a 24-hr period, although the difference in concentration between the beginning and end of sampling was not significant.

The concentrations of DIN and PO_4 were significantly higher in the lagoon than in the surrounding open water ($t = 4.002$; df = 63; $P < 0.001$ and $t = 2.725$; df = 63; $P < 0.01$, respectively) (Figure 4). There was not a significant inside-outside difference in SiO_4 concentration ($t = 1.987$; df = 47; $P > 0.05$).

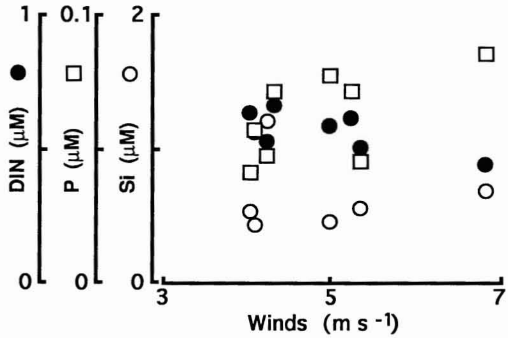

FIGURE 5. Relationship between wind speeds and concentrations of DIN ($NO_3 + NO_2 + NH_4$), PO_4, and SiO_4 in Davies Reef lagoon.

The average N:P and Si:N ratios inside the lagoon were 9.1:1 and 1.2:1, respectively, and those outside the lagoon were 5.4:1 and 2.1:1, respectively. As wind speeds decreased (i.e., 6 to 10 May), DIN concentration in the lagoon tended to increase, whereas PO_4 and SiO_4 concentrations showed an opposite trend (Figure 5).

Dinoflagellate abundance varied approximately six-fold during the monthly observations, with higher values being observed in summer months (November–April) (Figure 6). Chl. *a* concentration showed a similar trend, but was less variable than dinoflagellate abundance. The importance of dinoflagellates in lagoon phytoplankton communities appeared to increase as the relative availability of Si to N became less than the uptake ratio of Si:N in diatoms (i.e., 1:1, Redfield 1958) (Figure 7).

A list of 176 dinoflagellate species in GBR shelf waters was reported by Revelante et al. (1982). Their list, however, did not include *Prorocentrum minimum* (Pavillard) Schiller (15–25 µm) (cf. Dodge 1975) and *P. lima* (Ehrenberg) Dodge (25–35 µm). These two *Prorocentrum* species and small *Gymnodinium* spp. and *Scrippsiella* spp. (15–20 µm) were abundant in January and April samples, accounting for ca. 45–70% of the population. Scanning electron microscope observations revealed that two forms (round and ovoid) of *P. minimum* coexisted.

DISCUSSION

DIN concentration is significantly higher in the Davies Reef lagoon than in the surrounding shelf water. The extent of DIN enrichment in the lagoon seems dependent on wind conditions, which strongly influence the residence time for the lagoon water. Pickard

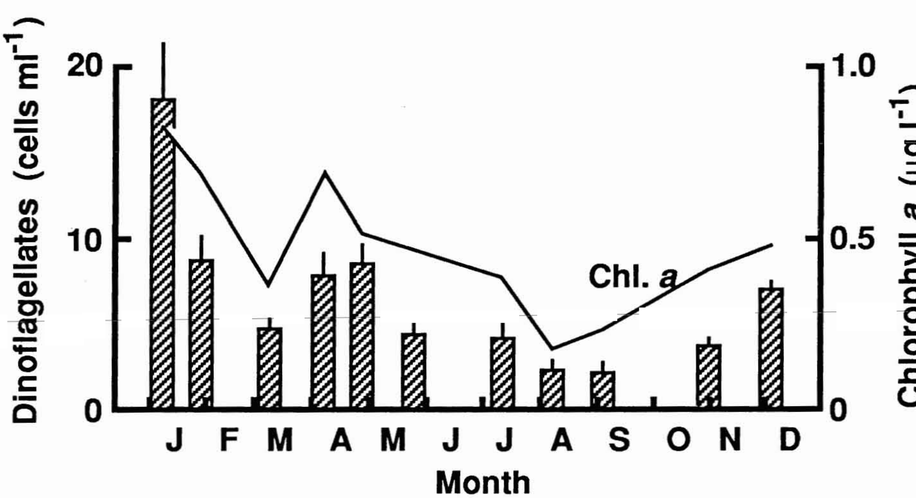

FIGURE 6. Seasonal variations in depth-averaged dinoflagellate abundance and chlorophyll *a* concentrations in Davies Reef lagoon. Vertical lines denote standard deviation of the mean.

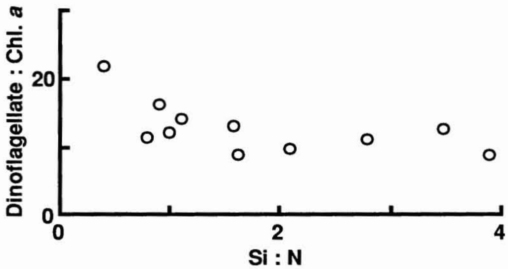

FIGURE 7. Relationship between dinoflagellate: chlorophyll *a* and Si:N ratios in Davies Reef lagoon.

(1986) estimated that residence time for the lagoon water is <2 days under medium to strong wind conditions (>5 m sec^{-1}), but may extend up to 6 days under light wind conditions.

The fixation of atmospheric N by benthic algal communities can have a strong influence on the N budget of coral reefs (e.g., Johannes and Project Symbios Team 1972, Wiebe et al. 1975, Larkum et al. 1988). However, the observed high DIN concentration in the lagoon is not always due to the DIN supply through excretion by N-fixing algae and nitrification by associated bacteria. Rather, the interstitial water in reef frameworks is enriched with DIN, particularly with NH_4 (e.g., Andrews and Muller 1983, Sansone 1985, Tribble et al. 1990). This large DIN pool seems to be supported by the transport of organic matter through advective flow and vertical mixing of water and the subsequent remineralization through both aerobic and anaerobic processes (Parnell 1986, Buddemeier and Oberdorfer 1986, 1988). Reef sediments also constitute a large N sink (Entsch et al. 1983), being maintained by the export of particulate organic matter from windward reefs (Johannes 1967, Marshall et al. 1975). The flux of regenerated DIN from these two internal sources probably explains a large proportion of the observed high DIN concentration in the lagoon. It should also be noted that the observations on 5 January and 5 April were carried out under very calm conditions (<3 m sec^{-1}), which were preceded by strong winds (up to 20 m sec^{-1}). The elevated DIN concentration on these two occasions may be due to stimulated DIN release from reef frameworks and sediments via wind-induced waves and vigorous mixing of water.

The lagoon and shelf systems apparently differ in terms of the relative abundance of inorganic nutrients. N:P ratios in GBR shelf waters are consistently <16:1 (e.g., Bellamy et al. 1982, Furnas and Mitchell 1984). This is usually the case for the lagoon water and is indicative of N limitation. However, the ratios became >16:1 under light wind and low flushing conditions. A buildup of phytoplankton populations was observed under such conditions (Furnas et al. 1990; this study). The results of the diel observations suggest that the internal DIN flux is high enough to balance with increased algal uptake and dilution by the surrounding shelf water, but the internal fluxes of P and Si are not.

In GBR shelf water, Si is available in excess of the requirement of diatom growth (Revelante and Gilmartin 1982, Furnas and Mitchell 1986). Extensive measurements of nutrient levels in and from rivers generally show rather high Si:N ratios (2–50), with lower values being observed during high discharge (A. W. Mitchell, M. J. Furnas, and M. Skuza, in prep.). In the lagoon, Si:N ratios are usually >1:1, but conditions do exist where nondiatom phytoplankton outcompetes diatoms (Si:N <1:1). Dinoflagellates are much more abundant in the lagoon (1.38–23.06 cells ml^{-1} [this study]) than in the GBR shelf water (0.01–3.8 cells ml^{-1} [Revelante and Gilmartin 1982]) and their proportion to the total phytoplankton biomass (chl. *a*) tends to increase with decreasing relative Si availability in the lagoon.

There is a clear summer-winter difference in nutrient concentration in the GBR shelf water (Revelante and Gilmartin 1982). A number of workers have demonstrated the seasonal cycle of reef benthic producers (e.g., Barnes 1988, Klumpp and McKinnon 1989). These two factors are potentially able to affect the nutrient concentration in the lagoon. Even if this is the case, however, it is difficult to detect the seasonal variation in nutrient concentration in reef waters through sampling at 1 month or longer intervals (Hatcher and Hatcher 1981, Furnas et al. 1990; this study) because of the large, short-term variation. Frequent sampling is one simple solution for this problem. If frequent sampling is not feasible, the collection of detailed weather data is vital to cope with this problem, because events associated with light to strong wind cycles seem largely responsible for the observed variation in nutrient concentration.

The question of whether organic production is limited by N or P stems from the difference in advective throughputs among systems (Smith 1984). For instance, if water exchange is greatly restricted, PO_4 as well as SiO_4 can become depleted in reef lagoons, whereas DIN may be supplied continuously from the atmosphere by N-fixing reef organisms. Thus the effect of further N or P loading on phytoplankton communities and related processes may differ among individual reef lagoons in the GBR, depending on their size and morphology, predominant winds, tidal range, and other factors. A similar argument may be extended to the northern, central, and southern GBR shelves with different hydrographic characteristics. The management of the GBR must encompass a range of flexible actions based on firm understanding of hydrographic and biological processes from single reef to shelf scale.

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